

RESEARCH ARTICLE

Low metabolism in a tropical bat from lowland Panama measured using heart rate telemetry: an unexpected life in the slow lane

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SUMMARY

Animals must optimize their daily energy budgets, particularly if energy expenditures are as high as they are in flying animals. However, energy budgets of free-ranging tropical animals are poorly known. Newly miniaturized heart rate transmitters enabled this to be addressed in the small, energetically limited, neotropical bat *Molossus molossus*. High-resolution 48 h energy budgets showed that this species significantly lowers its metabolism on a daily basis, even though ambient temperatures remain high. Mean roosting heart rate was 144 beats min⁻¹, much lower than expected for a 10 g bat. Low roosting heart rates combined with short nightly foraging times (37 min night⁻¹) resulted in an estimated energy consumption of 4.08 kJ day⁻¹, less than one-quarter of the predicted field metabolic rate. Our results indicate that future research may reveal this as a more common pattern than currently assumed in tropical animals, which may have implications in the context of the effect of even small temperature changes on tropical species.

Key words: resting metabolic rate, energy expenditure, *Molossus*, foraging strategy, social foraging, torpor.

INTRODUCTION

A large part of animals' lives is characterized by the effort to maximize energy intake while minimizing energy investment in order to accumulate energy for reproduction and times of shortage. Animals must spend time and energy to find and exploit resources and this investment increases with unpredictability and limited availability of resources. Although flight is the fastest way to cover distance and reach resources, it is also the most expensive mode of locomotion per unit of distance covered (reviewed in McNeill, 2002; Schmidt-Nielsen, 1997). In both bats and birds, energy consumption during flight is up to 15-fold higher than that during resting (Carpenter, 1986; Masman and Klaasen, 1987; Speakman and Thomas, 2003; Winter and von Helversen, 1998). Consequently, we predict that meeting their energetic demands might be difficult for flying animals with a specialized foraging niche, high cost of flight and rare and/or unpredictable prey, even on a daily basis.

Bats offer an excellent model system to test this prediction. They fly and the morphology of each foraging guild (or functional group) is highly adapted to the corresponding foraging niche (Norberg and Rayner, 1987). The morphology of bat species that forage for insects in open space is particularly strongly adapted to this strategy. They have long, narrow wings that are suited to fast flight and covering long distances, but they also have high wing loadings, which incur high energetic costs compared with more maneuverable species with low wing loadings that forage close to the substrate (Norberg and Rayner, 1987). Many open-air foragers are specialized on insect swarms (Safi and Kerth, 2004), a food source that is abundant when found, but unpredictable in time and space. In addition, insect swarms often occur only during a small time window, usually just after sunset (Jones and Rydell, 2003). At least some species increase foraging efficiency for this resource by group hunting, indirectly

searching a larger area for insect swarms by flying within earshot of roost members and eavesdropping on their echolocation calls (Dechmann et al., 2009; Dechmann et al., 2010). Because of the temporally limited availability of insect prey, some of these species also have short daily activity periods of 1 h or less (Dechmann et al., 2009; Dechmann et al., 2010). They cope with up to 23 h of fasting a day by fuelling flight immediately with lipids from ingested insects (Voigt et al., 2010). Nonetheless, the question arises how these animals budget their energy over the course of the day. They must balance the cost of high energy expenditure during flight with acquiring all the food needed during one or two short activity bouts. One way to do this would be to employ compensation strategies during the long periods that they spend inactive in day roosts.

In addition to high energy expenditures of flight, small animals, including bats, have relatively high resting metabolic rates and thermal conductances, which should aggravate their energetic dilemma (Speakman, 2000; Speakman, 2005). As an adaptation to this, many bat species reduce their metabolic rate and use torpor to conserve energy (Speakman and Thomas, 2003). Most work in this context has focused on thermoregulation by bats in the temperate zones (e.g. Chruszcz and Barclay, 2002; Cryan and Wolf, 2003; Hamilton and Barclay, 1994; Kurta, 1991; Kurta et al., 1990; Lausen and Barclay, 2003), but subtropical or even tropical bats are also known to use torpor and even hibernate (e.g. Bartels et al., 1998; Cory Toussaint et al., 2010; Geiser and Brigham, 2000; Hosken and Withers, 1997; Kelm and von Helversen, 2007). However, field data on the thermal biology of tropical bats are scarce, even though torpor is thought to have evolved in the tropics (McNab, 1969).

To date, most studies of bat energetics have experimentally evaluated energy use by collecting respirometry data while

manipulating temperature or food availability in captive animals. The variable most commonly used for comparing metabolic rates within and between taxa is resting metabolic rate (RMR), i.e. the metabolic rate of post-absorptive, resting animals within the thermoneutral zone. Empirical evidence shows that RMR does not scale linearly with other, more energy-consuming behaviours and that field metabolic rates (FMRs) give a more reliable picture of overall energy consumption (Speakman, 2005). Doubly labelled water is the most commonly used method to assess energy expenditure in the field or under semi-natural conditions (McLean and Speakman, 1999; Schmid and Speakman, 2000), and the available data show large differences between predictions made based on respirometry measurements in the laboratory and FMR values from free-ranging animals (Bevan et al., 1995; Coburn and Geiser, 1998). This is because energy consumption can fluctuate widely depending on the activity and foraging success of the animal, but this is hard to predict from RMR.

Detailed studies on the energy budgets of free-ranging bats remain scarce, largely because of a lack of suitable technology to measure parameters of these small animals in the field. Heart rate transmitters, which have been available for several years (Butler et al., 2002; Froget et al., 2004; Green et al., 2001; Studier and Howell, 1969) have only recently become miniaturized enough to measure heart rate in small animals, such as most bats, in the field (Steiger et al., 2009). Data from heart rate telemetry can, if calibrated, be directly converted into estimations of energy consumption and may be more powerful than the doubly labelled water method for detecting hypometabolic states, including torpor, because the data have higher temporal resolution (Bowlin and Wikelski, 2008; Nolet et al., 1992). In addition, this method does not require recapture of the animals, which is often difficult or impossible in free-ranging bats.

We used the neotropical Pallas' free-tailed bat *Molossus molossus* (Pallas 1766) to understand the energy use of small mammals facing energy constraints in the field. This bat forages socially, which might significantly increase efficiency; however, it is also a morphologically specialized open-aerial insectivore and feeds during a short activity period of approximately 1 h (Dechmann et al., 2010). We evaluated how the high estimated energy consumption during flight and the short time spent foraging might balance out as reflected by the metabolic rates during the rest of the day. We expected that bats that spent more time flying at night would need to reduce metabolism more in the roost to make up for the higher energy expenditure. To put our results in context, we calculated estimated energy expenditure based on heart rate values and compared these with the values predicted in the literature for a bird, a terrestrial mammal and a bat of the same size. Our results for this species should provide insights about energy allocation in the tropics, where factors other than temperature likely play a major role in how energy is allocated.

MATERIALS AND METHODS

Animals, study site and transmitter attachment

We conducted our study in and near the village of Gamboa, Panama (09.07N, 079.41W), where the Smithsonian Tropical Research Institute (STRI) has a field station. Gamboa is surrounded by semi-deciduous tropical lowland rainforest, and has a distinct wet and dry season (Windsor, 1990). Daily mean (\pm s.d.) ambient temperature during the study period was $27.5 \pm 2.0^\circ\text{C}$. The mean daily maximum was $31.1 \pm 1.6^\circ\text{C}$ (range = 26.8 – 33.1°C) whereas the mean daily minimum was $25.2 \pm 0.6^\circ\text{C}$ (range = 24.2 – 26.3°C). Temperature data (collected every 15 min) were obtained from STRI's Physical Monitoring Program. Sunrise (06:13–06:19 h) and sunset (18:27–18:28 h) during the study period were calculated with the

sunrise function in the R *maptools* package (<http://cran.r-project.org/web/packages/maptools/maptools.pdf>).

We caught bats in mist nets (Ecotone, Gdansk, Poland) as they emerged from daytime roosts in houses after sunset on 26 and 29 March and 2 April 2010. We placed bats in cloth bags and processed them as soon as bats ceased leaving the roost. We measured forearm length to the nearest 0.01 mm with calipers (Mahr, Göttingen, Germany), mass to the nearest 0.25 g (Pesola, Baar, Switzerland), and recorded sex, age and reproductive status. We selected seven adult female bats from three roosts (roost A: one individual; roosts B and C: three individuals each) for telemetry. They weighed 10.8 ± 0.4 g (mean \pm s.d.).

We tracked bats with heart rate transmitters (~ 0.6 g; SP2000 HR, Sparrow Systems, Fisher, IL, USA), which we attached to the back of the bats. The transmitters emitted a continuous long-wave signal that was frequency-modulated by cardiac muscle potentials (see Cochran and Wikelski, 2005). We trimmed the fur in the middle of the back between the shoulder blades. Then we used a topical analgesic (xylocaine spray, Astra Zeneca, Wedel, Germany) and, after disinfecting the back of the bats with alcohol, the transmitter's two electrode gold wires were also disinfecting and inserted ca. 3 mm dorsally through a ca. 1 mm incision in the skin. The transmitters were then glued over those incisions, thus sealing them from the air, using a combination of superglue (Krazy Glue, Elmers, IL, USA) and eyelash adhesive (Andrea glue, American International Industries, Commerce, CA) (Cochran and Wikelski, 2005). Superglue has the same ingredients as surgical glue and has been used in our group for several years with no detrimental effects on any animals. The electrodes are highly flexible and do not appear to disturb the animals. When the transmitter falls off the animal after a maximum of 4 days, the electrodes slide out, leaving no visible scars as confirmed by observations on birds and bats in captivity and recaptures in the field (M.W., personal observation) (Steiger et al., 2009).

Calibration of heart rate versus oxygen consumption

We measured rates of oxygen consumption (V_{O_2}) and carbon dioxide production (V_{CO_2}) of six of the seven bats we tracked in an open-flow, push-through respirometry system. External air ($>75\%$ humidity, $\sim 25^\circ\text{C}$) was pumped through a mass flow controller (TR-FCI, Sable Systems, Las Vegas, NV, USA) and a multiplexer (V2-0, Sable Systems) into a 1 liter respirometry chamber. To minimize stress during the measurements, we did not use a smaller metabolic chamber or higher flow rate (M.W., unpublished data). As a control, we measured the empty chamber before putting in each bat. Bats were able to move freely, but not fly, in the chamber. Flow rate was adjusted to 1400 ml min^{-1} , allowing for 95% equilibrium within 1.26 min, or 99% equilibrium within 3.3 min. To dry the air leaving the chambers we used a Peltier-Effect Condenser (PC-1; Sable Systems). A sub-sample of the air flowing out of the respirometry chambers was used to determine CO_2 concentration (CA-1B, Sable Systems). After scrubbing potentially remaining water from the air with Drierite we determined V_{O_2} (FC-1B, Sable Systems). We did not observe leaks in the respirometry system as confirmed by pressurizing the chamber.

We estimated instantaneous oxygen consumption using the equation described by Bartholomew and co-authors (Bartholomew et al., 1981), after empirically determining the Z-value (the denominator of Bartholomew's equation). The mean (\pm s.d.) Z-value was 0.25 ± 0.1 . We then used eqn 3b from Withers (Withers, 1977) to determine V_{O_2} . We used the respiratory quotient (RQ) – defined as the ratio of CO_2 produced to O_2 consumed – to calculate the

thermal equivalents and metabolic rates (kJ day^{-1}) following Walsberg and Hoffman (Walsberg and Hoffman, 2005). After completion of the metabolic measurements we released all bats at the roost within 4 h of capture.

Heartbeats of bats in the respiratory chamber were recorded as a sound file onto a laptop computer (see below). V_{O_2} and simultaneous heart rate data were obtained from each bat at five to six random time points that were at least 2 min apart (range=2.1 to 15 min, mean \pm s.d.=7.8 \pm 3.2 min, $n=31$) to account for potential temporal autocorrelation effects. After a maximum of 4 h, we released all bats at the site of capture. We used a mixed model in R (<http://cran.r-project.org/web/packages/lme4/lme4.pdf>) with heart rate as a linear predictor of estimated energy expenditure, correcting for the effect of individual on the intercept by entering each bat as a random factor (see also Bevan et al., 1994; Green et al., 2001).

Heart rate telemetry and analysis of estimated field energy expenditure

After releasing them, we recorded the heartbeat of the seven free-ranging bats during the consecutive 48 h. We used telemetry receivers (AR8200, AOR, Tokyo, Japan) connected to Yagi antennae (Sparrow Systems) to detect the signal of the transmitter, which was recorded on a digital voice recorder (VN-2100PC/WS-400S/VN 4100, Olympus, Tokyo or R09HR, Edirol, Bellingham, WA, USA). Teams of two to three persons were positioned directly outside each roost, continuously adjusting the antennae positions to optimize signal reception. We recorded the signal at least 10 s every 5 min and determined instantaneous heart rate by counting and timing an average of five beats for each recording (Steiger et al., 2009).

Molossus molossus has one or two daily foraging sessions: just after sunset and sometimes just before sunrise. This species usually spends all time outside the roost flying (Dechmann et al., 2010). Sometimes, one or both of the foraging sessions may be skipped during a particular night, for example when it rains. The length of foraging sessions and thus time spent flying was defined as the time between the last reception of a bat's signal in the roost until the first detection of the stationary bat in or near the roost (see also Dechmann et al., 2010). Thirty minutes before sunset and 1 h before sunrise we positioned additional teams of two to five persons on a canopy tower near Gamboa. Those teams recorded heart rates of flying bats whenever possible until all individuals had returned to the roost.

We analyzed the recorded sound files with Cool Edit 2000 (Syntrillium Software, Phoenix, AZ, USA) following Cochran and Wikelski (Cochran and Wikelski, 2005). For most analyses we did not use the data from the capture night, as they may have been influenced by the fact that we released the bats after their natural evening foraging session. Instead, we started data analysis with data recorded after the subsequent sunrise.

We investigated daily patterns in heart rate from recordings taken when the animals were inside their roosts with general additive mixed models (GAMMs; R package mgcv) (Wood, 2004), using log-transformed heart rates and individual as random factors. These models account for temporal autocorrelation and the circular nature of data collected during 24 h periods, allowing modelling of the data without *a priori* expectations about the relationship of the data with time of day. We used the same model to describe potential patterns in heart rate over time. To assess whether daily patterns in heart rate might be influenced by temperature, we used the same model with air temperature instead of time of day as an explanatory variable and compared the two models using Akaike's information criterion (AIC) for goodness of fit.

We compared the mean heart rate per bat for day and night with a paired Wilcoxon test. In addition, we determined a mean flying heart rate for all bats combined. No individual values were calculated, as we were only able to make brief recordings of most bats during flight.

Based on the respirometry calibration and the observed duration of time in the roost and foraging sessions, we estimated resting and flying metabolic rate as well as daily total energy expenditure and energy spent flying. Additionally, we calculated the mean estimated total daily energy expenditure (DEE) in the same manner as described above, using mean flight duration and heart rate of all bats.

Comparison with existing scaling relationships

In both mammals and birds there is a significant positive scaling relationship between body mass and the basal metabolic rate (BMR) (Speakman, 2000; Speakman and Thomas, 2003). We calculated 95% confidence intervals from the published data and compared this with our observed mean RMRs. For comparison with other mammals and birds, we plotted published means (Speakman, 2005) against the mean of our data from *M. molossus*.

Statistical analyses

We used R version 2.12.0 for all statistical analyses (R Development Core Team, 2010) and present results as means \pm 1 s.d. unless otherwise stated.

RESULTS

Calibration of heart rate versus oxygen consumption

We measured oxygen consumption for six of the seven bats we tracked (bats 2–7) and selected 31 independent (separated by >2 min) measurements (see Materials and methods). Mean mass of the bats used for the calibration was 10.8 \pm 0.4 g. The mean RQ was 0.87 \pm 0.05. The mean thermal equivalent was 20.11 \pm 0.21 $\text{kJ l}^{-1} \text{O}_2$. Oxygen consumption ranged from 6.0 ml h^{-1} at a heart rate of 110 beats min^{-1} to 64.0 ml h^{-1} at a heart rate of 980 beats min^{-1} . A significant linear relationship (Nagelkerke $R^2=0.84$) was found in a mixed model between heart rate and oxygen consumption (d.f.=24, $t=16.1$, $P<0.001$), controlling for individual. Regression of DEE (kJ) against heart rate (f_H ; beats min^{-1}) using random effects for the individuals in a mixed model yielded the following equation (see also Fig. 1):

$$\text{DEE} = 0.028f_H + 0.287. \quad (1)$$

Heart rate telemetry and analysis of estimated field energy expenditure

We recorded heart rates of seven free-ranging adult female *M. molossus* from three different roosts for at least 48 h each. It was difficult to obtain good recordings from flying bats. Therefore after excluding bad-quality recordings, we analyzed a total of 2119 5 min sequences for roosting bats (Table 1), but only 25 from flying bats. Depending on the quality of the sound recordings, there were varying amounts of missing data (see Fig. 2 for plots of all bats and Table 1 for roosting data).

The mean daily duration of flight was 33.7 min (Table 1), which is similar to published values (Dechmann et al., 2010). The mean heart rate of flying bats was 846.6 \pm 171.1 beats min^{-1} ($N=25$, range=595–1245 beats min^{-1}). Most bats foraged once every evening. Two bats (bats 4 and 7) also foraged in the morning, but only the morning after they had been captured. They did not spend more time flying in total than any of the other bats, thus overall energy

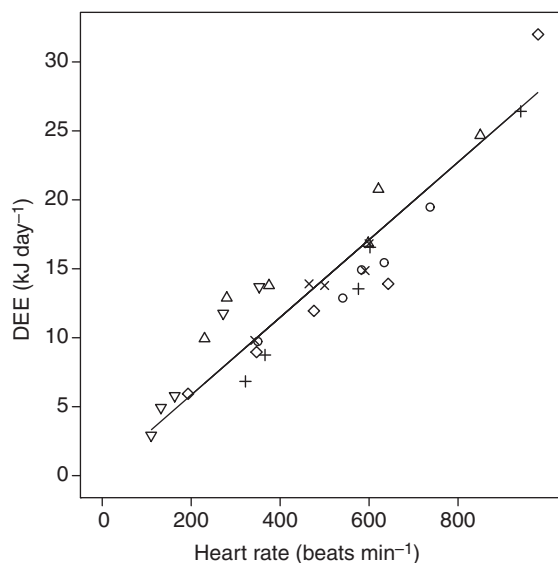


Fig. 1. Relationship between heart rate (beats min^{-1}) and estimated daily energy expenditure (DEE; kJ day^{-1}) based on respirometry data for six adult female *Molossus molossus*. Symbols represent individual bats.

budgets were only affected by the time spent flying and we excluded data until first sunrise from most analyses (see above).

Bats in the roost had a mean heart rate of $143.7 \text{ beats min}^{-1}$ (range=42–756 beats min^{-1} ; Table 1). Heart rate was not normally distributed. The median was $128.8 \text{ beats min}^{-1}$ and values above 290 and lower than 60 were rare (Fig. 3).

There was considerable variation in individual heart rates (Fig. 2). Most bats had fluctuations throughout the day (bat 3 in Fig. 2), but the daily pattern of other bats contained periods of relatively constant low heart rates (bat 7, Fig. 2). High heart rates of roosting bats lasted only 5–10 min and heart rate changed rapidly without transition. The GAMM described a pattern over the course of the day (Fig. 4) of heart rate being slightly elevated around the time bats left to forage in the evening. However, the random coefficient, which addresses individual variation, shows that apart from bat 1, whose rate was a bit lower than the others, all bats had similar heart rates and thus energy budgets. The model that also included air temperature yielded an AIC more than 30 points higher than the one using time of day. Therefore, time of day is a better predictor of daily patterns in heart rate.

During the day, mean heart rate ($134 \pm 53.7 \text{ beats min}^{-1}$) was lower than at night ($155.7 \pm 70.3 \text{ beats min}^{-1}$), but not significantly so

(Wilcoxon matched-pairs signed ranks test, $V=4$, $P=0.11$). Only bat 4 had a higher heart rate during the day (Table 1).

There was a significant positive correlation between the amount of time bats spent foraging and their heart rate in the roost (Spearman rank, $r_s=0.90$, $S=5.55$, $P=0.006$ and $r_s=0.90$, $S=5.55$, $P=0.006$; $N=7$).

Comparison with existing scaling relationships

We calculated the estimated DEE for the bats we tracked using the mean heart rate of the GAMM model. The result was 4.08 kJ day^{-1} . If we added the higher energy expenditure during flight we obtained a DEE of 4.55 kJ day^{-1} . The published BMR for a generic bat of the same body mass as our study animal ($M_b=10.8 \text{ g}$) is 8.4 kJ day^{-1} (Speakman and Thomas, 2003). The roosting metabolic rate ($4.082 \text{ kJ day}^{-1}$) of *M. molossus* in our study was thus lower than expected, falling far outside the 95% confidence interval of the regression. The difference between the observed and expected values increased when we compared the published field metabolic rate for bats ($37.18 \text{ kJ day}^{-1}$) (Speakman and Thomas, 2003) with our estimate of 4.55 kJ day^{-1} for *M. molossus*. The large difference is partly caused by the short flight times of *M. molossus* and may have additionally been underestimated because of the small sample size and calibration with non-flying animals.

Similarly, DEE predictions of a generic 10.8 g mammal ($10.97 \text{ kJ day}^{-1}$) and bird ($16.85 \text{ kJ day}^{-1}$) (Speakman, 2005) were also higher than the mean DEE estimates for *M. molossus*. Note, however, that data used to estimate *M. molossus* metabolic rates include all data from roosting bats. Thus they might contain high metabolic rates caused by activity within the roost in addition to the resting metabolism.

DISCUSSION

In animals from several taxa there is a negative relationship between body size and energy consumption per unit body mass (Hayssen and Lacy, 1985). Smaller animals consume relatively more energy. This relationship becomes even steeper in flying animals. Flapping flight (Sapir et al., 2010) is up to 15 times more energy consuming than rest (McNeill, 2002; Schmidt-Nielsen, 1997). Therefore, we expected that even if energetically limited by morphology and foraging niche, the energy expenditure of our 10 g study species would be high, and that this would be reflected by its heart rate. Most published work on the energy consumption of bats has focused on the occurrence of torpor in temperature-manipulated respirometry studies of captive and (usually) fasted animals (Bartels et al., 1998; Hosken and Withers, 1997; Kelm and von Helversen, 2007) or free-ranging individuals carrying temperature-sensitive transmitters

Table 1. Summary of individual heart rate data for *Molossus molossus*

ID	Mass	N	Roosting heart rate (beats min^{-1})					Flight time (min)		
			Min.	Max.	Mean \pm s.d. (day)	Mean \pm s.d. (night)	Mean q (day + night)	Random coefficient	Total	Excluding first night
1	11	327	64.5	278.6	108.0 ± 25.9	111.1 ± 35.6	109.1 ± 29.6	0.79	26	26
2	11	304	60.9	430.4	146.5 ± 41.8	167.0 ± 72.6	156.9 ± 60.3	1.07	190	154
3	10	412	51.0	755.7	123.7 ± 35.9	143.9 ± 93.3	133.2 ± 69.8	0.95	79	60
4	11	337	62.8	487.8	167.0 ± 77.6	138.3 ± 38.1	156.0 ± 66.8	1.06	109	80
5	11	213	48.5	458.5	150.0 ± 55.7	188.3 ± 57.5	162.9 ± 59.0	1.11	190	120
6	11	253	61.6	392.7	134.4 ± 45.7	173.9 ± 61.2	153.4 ± 57.1	1.03	154	60
7	11	273	42.0	382.2	114.7 ± 48.2	180.5 ± 62.8	146.7 ± 64.7	1.01	125	55
All bats (mean)	10.8	302.7	42.0	755.7	134.0 ± 53.7	155.7 ± 70.3	143.7 ± 58.2	1.00	125	79

Roosting heart rate data exclude the first night. N, data points. Random coefficient: deviation of this individual's overall heart rates from the mean calculated by the model; overall heart rate means are calculated from the total data set, not as means of individual means.

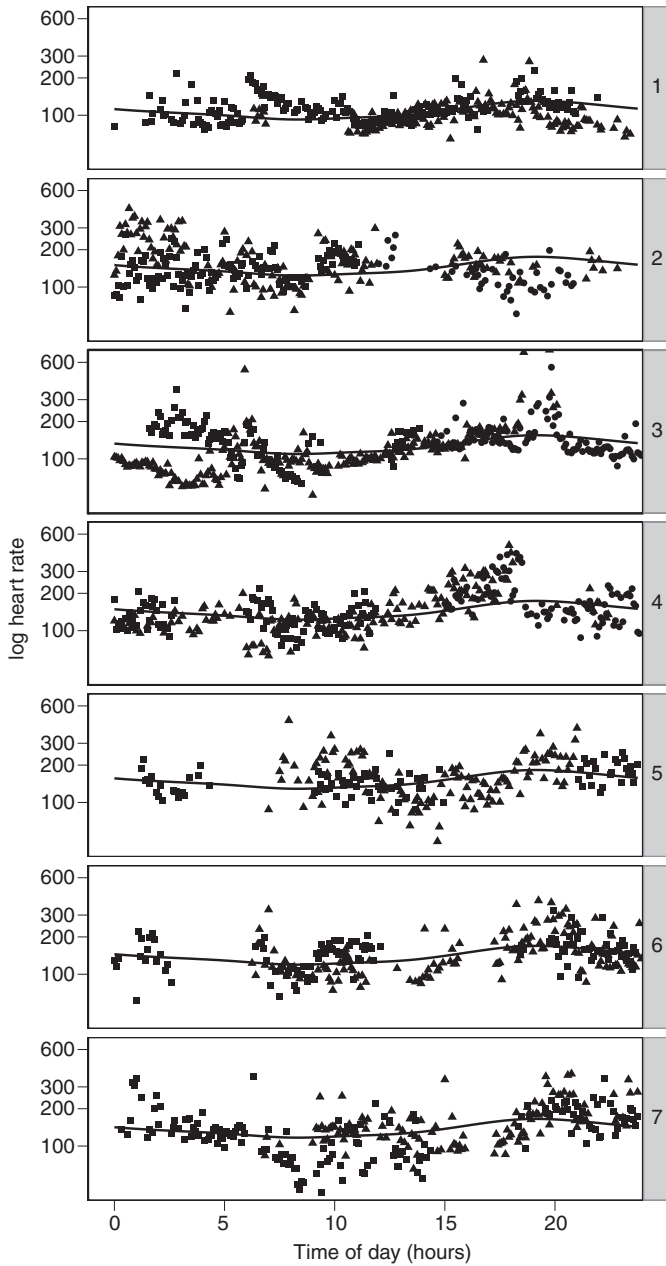


Fig. 2. Forty-eight hour measurements of all seven tracked bats averaged over 24 h. Each data point represents a measurement from a 5 min slot (no flight values were included). Note the rapid changes in heart rates from one data point to the next. Different symbols represent the day on which data were collected (up to 3 days in each 48 h period).

(Audet and Thomas, 1996; Turbill et al., 2003). In our study we were expecting to find high DEE values because as a tropical species, living near the equator at relatively consistent high ambient temperatures, *M. molossus* should be limited in its ability to use torpor, unlike bats from regions with stronger seasonal and daily temperature fluctuations (Bonaccorso et al., 1992; Cory Toussaint et al., 2010; Speakman and Thomas, 2003).

In stark contrast to our prediction, we found low mean heart rates (Leitner, 1966; Leitner and Nelson, 1967) corresponding to DEE values only half of published values for BMR of the same-sized bats and one and a half times less than that of a terrestrial mammal (Speakman, 2000; Speakman and Thomas, 2003). This difference

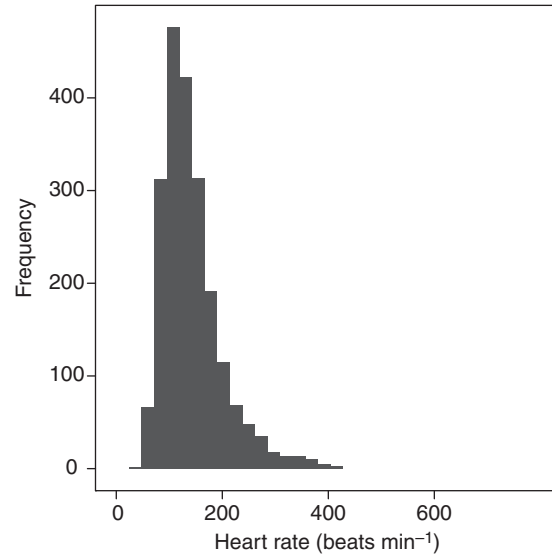


Fig. 3. Frequency distribution of heart rates for seven bats while roosting.

became even more pronounced when we compared our values with published FMRs, especially those including flying activity, of other bats. In fact, comparable FMRs, predicted from measurements with doubly labelled water for a 10 g bat would be almost 10 times higher than what we recorded in *M. molossus*.

This raises questions about the potential validity of our data. However, our calibration *via* indirect calorimetry (measurements of O₂ consumption and CO₂ production) at a broad range of heart rates for six of our seven animals produced a highly significant predictive relationship. In addition, heart rate values during flight were within the expected range of 600–1200 beats min⁻¹ (Studier and Howell, 1969). That, in conjunction with the consistency between individual bats (see Table 1), suggests that our data are representative of the animals' metabolism, at least within the limits of the method (i.e. mainly the necessity to be within range of the transmitters, the need for calibration and the work-intensive analysis) (Butler et al., 2004; Speakman, 2000). However, we underestimate the energy expenditure during flight if bats show a steep increase in energy consumption during powered flight, similar to birds (Butler et al., 2004). Nevertheless, because of the short flight times in molossid bats, we expect that our estimate of DEE is not overly biased.

How can it be then, that *M. molossus*' heart rates and correlated energy expenditures are so low? There are two, non-exclusive explanations for this. One is that the combination of foraging strategy and morphology, which results in an energetically extremely expensive lifestyle, is compensated by lowering energy consumption during roosting. The other is that our results may not be as much of an exception as they seem. *Molossus molossus*, as an open-aerial forager with narrow wings and high wing loadings, probably spends proportionally more energy during flight than most other bat species (Norberg and Rayner, 1987). This specialized morphology makes these bats much less flexible foragers than broader-winged species. Broad-winged bats can switch to foraging in gaps and along edges if needed. In contrast, narrow-winged bats usually exploit abundant food resources that occur during short time windows, especially insect swarms (Safi and Kerth, 2004). During most parts of the night, insects in mid-air may simply not be abundant enough to justify the energy expenditure required to find and capture them for narrow-winged bats. Recent work suggests that one strategy to exploit these insect swarms at dusk more efficiently is to use the information

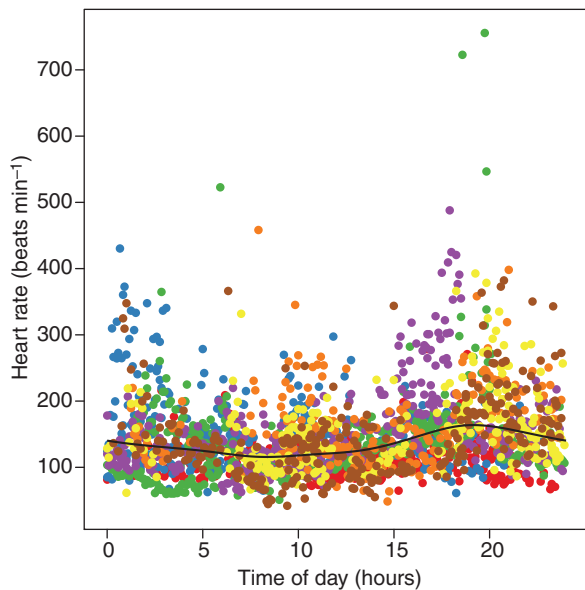


Fig. 4. General additive mixed model of heart rate data for roosting bats over a 24 h period (black line). The y-axis is back transformed from the log scale. Different colours represent different individuals.

content in group members' echolocation calls during foraging, which results in coordinated foraging by group members (Dechmann et al., 2009; Dechmann et al., 2010). Nonetheless, insect swarms usually occur only during approximately 1 h around sunset and this results in extremely short foraging periods for species specialized on this food source (Dechmann et al., 2009; Dechmann et al., 2010; Safi and Kerth, 2007). Lowering energy expenditure during the long fasting intervals must be sufficient to leave them with enough energy stores to go foraging again and even, in the case of rain, sometimes entirely skip a night of foraging (Dechmann et al., 2010). This may have been a strong enough selective pressure for these bats to evolve lower metabolic rates and correlated energy consumption.

The low DEE we found is even more surprising in light of the fact that ambient temperatures stay consistently high in the study area and, like several members of this family of bats, *M. molossus* sometimes roost directly under corrugated tin roofs, which may become hotter than ambient temperature during the day (Maloney et al., 1999). Nonetheless, our data show that, as is typical for bats because of their nocturnal activity period (Bartels et al., 1998), metabolic rates of *M. molossus* are higher during the cooler night and that there is no influence of ambient temperature. In sugar gliders, bouts of true torpor are preceded by periods of lowered activity accompanied by a drop in body temperature of only 1.2°C, but resulting in significant energy savings (Christian and Geiser, 2007). For this reason we do not define the state of lowered heart rate in our bats as torpor, but simply as 'lowered metabolism', as currently there is a lack of a clear definition of this state.

The explanation that energy limitation in bats that forage in this particular manner may be a reason for low heart rates is consistent with the positive correlation between time spent flying and daily heart rate, but is not what we expected. In flying animals, even single flight events normally result in lower RMRs (Speakman and Selman, 2003). This is contradicted by our data. Although our sample size is small, we found that the longer individuals flew, the higher their roosting metabolic rates and DEE. Prolonged flight may be caused by longer availability of insects, leading to more food

intake, and thus allowing the bats to spend less time at low heart rates.

It remains to be determined what the costs of these low heart rates are. However, any such cost may be reduced by the fact that by lowering metabolism without a significant drop in body temperature the bats remain mobile (see also Willis and Brigham, 2003) and are able react quickly to changes in environment, such as approaching predators, as suggested by the large and rapid changes in heart rates from one 5 min observation period to the next (see Fig. 2). Bats in deep torpor require up to several minutes of increased metabolic rate and muscle shivering before they can elevate their body temperature back to a level that allows them to fly, and torpor bouts have been defined to last at least 1.5 h (Geiser and Ruf, 1995).

Interestingly, none of the bats we equipped with transmitters were palpably pregnant (otherwise they would have been excluded for animal welfare reasons). However, given the time of year, it is likely that at least some were in early pregnancy. Studies of temperate zone bats assume that the main reason for the colonial lifestyle of females in the summer is that torpor reduces embryonic development and pregnant bats cluster to benefit from each others' body warmth until weaning, only entering deep torpor when forced by limited resource availability or extremely cold weather (Speakman and Racey, 1987; Speakman and Thomas, 2003; Willis et al., 2006). Whether this slowed embryonic development also applies to *M. molossus* and other, potentially energy-saving, tropical bats, which remain normothermic or at least do not reduce their body temperature very much, remains to be determined.

To judge whether low roosting heart rate is an exception or occurs in other species, additional field studies are warranted. Short-term reductions in metabolism through lowered heart rates may simply have been overlooked. Australian *Nyctophilus*, frequently entered torpor in the laboratory, but when monitored over long time periods it also exhibited BMRs that were up to 65% below predicted values. *Nyctophilus* sp. belong to a family of bats common in the Northern Hemisphere, where torpor occurs regularly even on a daily basis, and this change in metabolism was accompanied by a lower body temperature of 29.3°C (Geiser and Brigham, 2000). Given that we did not monitor body temperature, we cannot assess whether something similar may occur in *M. molossus*. Heart rate data for the spotted antbird, an understory bird occurring in the forest near our study area, suggests that this may be a more common phenomenon and not restricted to bats (Steiger et al., 2009). These birds also exhibit surprisingly low heart rates, mainly because they are much less active than previously assumed. It may be that with heart rate transmitters, future studies will show that many more tropical species are capable of hitherto unknown energy-saving strategies.

In addition to energy saving, the reduction of evaporative water loss may also be important for bats living at high ambient temperatures (Maloney et al., 1999). The fact that metabolic rates were reduced even more during daytime is consistent with the idea that downregulation of metabolic rate might limit evaporative water loss, especially during the heat of the day.

Future studies need to integrate the measurements of roost and body temperature of tracked bats with larger sample sizes and over longer time periods. Even though ambient temperature did not influence our model, small fluctuations in the roost temperature may have contributed to the changes in heart rate. Body temperatures usually change at a time scale of several minutes, and even respirometry data, which cannot be collected from free-ranging animals, do not provide insights into energetics at the temporal

resolution of heart rate measurements (Maloney et al., 1999). Fluctuations in heart rate, such as those found in the present study, might be part of the normal 'torpor' pattern, but may not have been described in the literature because measurements of torpor and metabolic rates are based on oxygen consumption and changes in body temperature (Cory Toussaint et al., 2010; Stawski et al., 2009). Smaller fluctuations in temperature have a much larger effect on tropical than on temperate species, at least in heterotherms, because they are adapted to more narrow temperature ranges in their environment (Dillon et al., 2010). Studies of energy-saving mechanisms in tropical animals may thus help to investigate whether they will be more sensitive to climate change than others, as predicted by Dillon and co-authors for heterotherms (Dillon et al., 2010).

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